**Number of flankers influences foveal crowding and contour
interaction differently**

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Abstract

Nearby flanking objects degrade visual resolution. If the flankers are similar to the acuity target, this influence is called crowding (CW), whereas if the flanking stimuli are simple bars then the phenomenon is known as contour interaction (CI). The aim of this study was to compare the influence of the number and position of flankers on foveal CW and CI to investigate possible differences in mechanism of these two effects.

Five normal observers viewed single, foveally presented Sloan letters surrounded by 1, 2 or 4 flankers (either a Sloan letter or one-stroke-width bars), presented at several edge-to-edge separations. Single flankers were presented in the right, left, top or bottom position, 2 flankers were placed equally to the right and left or top and bottom of the central target, and 4 flankers were equally spaced in all four directions. Percent correct letter identification was determined for each type, number, position and separation of flankers and confusion matrices were constructed for separations equal to 20% and 100% letter width.

Increasing the number of flankers caused an increase in the magnitude of both phenomena. CW showed a greater magnitude than CI for higher numbers of flankers. Analysis of confusion matrices suggests that in addition to the edge-to-edge interaction that appears to mediate CI, letter substitution and feature pooling contribute significantly to CW when higher numbers of flankers are presented.

Foveal CW is more strongly influenced by an increase in the number of flankers than CI, which can be explained by the presence of additional interaction effects.

Keywords

crowding, contour interaction, fovea, number of flankers, position of flankers, confusion matrices

1. Introduction

The presence of nearby flankers (contours, letters, etc.) has a deleterious effect on visual resolution and impairs single-letter identification (Flom, 1991; Levi, 2008; Pelli & Tillman, 2008; Whitney & Levi, 2011). This spatial interference is characterised by a lateral extent and magnitude. The lateral extent represents the farthest distance at which the surrounding flankers produce a criterion degradation of visual performance. The magnitude constitutes the maximum impairment in resolution or letter identification compared to the condition with no flanking targets. If the flankers are similar to the acuity target, the spatial interference has been called “crowding” (CW) (Flom, 1991; Flom, Weymouth, & Kahneman, 1963), whereas if the flanking stimuli are simple bars then the phenomenon is known as contour interaction (CI) (Flom, 1991; Flom, Weymouth, & Kahneman, 1963; Takahashi, 1968). In the case of CW, the flankers are more complex and may include bar elements. Thus, CI can be considered tentatively as a part of or at least a contributing factor to CW.

Foveal CI (Bedell, Siderov, Waugh, Zemanová, Pluháček, & Musilová, 2013; Danilova & Bondarko, 2007; Musilová, Pluháček, Marten-Ellis, Bedell, & Siderov, 2018; Siderov, Waugh, & Bedell, 2013) and CW (Coates, Levi, Touch, & Sabesan, 2018; Formankiewicz & Waugh, 2013; Pluháček & Siderov 2018) occur only within a fixed angular range of letter-to-flanker separations irrespective of the letter size; this range is similar for both effects. Moreover, recent studies indicate that CI and CW differ minimally, if at all, for foveal vision in adults (Danilova & Bondarko, 2007; Marten-Ellis & Bedell, in press; Norgett & Siderov, 2014). These observations suggest that both foveal CI and CW have a similar neural origin. Foveal CI is considered by many authors to result from the antagonistic structure of the neural receptive fields in the visual pathway (Bedell et al., 2013; Danilova & Bondarko, 2007; Flom, Weymouth, & Kahneman, 1963; Latham & Whitaker, 1996; Musilová et al., 2018; Wolford & Chambers, 1984). Reports by Pluháček & Siderov (2018) and Marten-Ellis & Bedell (in press) that, similar to foveal CI (Bedell et al., 2013; Musilová et al., 2018), foveal CW weakens with decreasing stimulus luminance indicates that CW can be at least partly explained in the same way.

In contrast, CI and CW differ markedly in the visual periphery. In the case of CW, letter recognition for small target-to-flanker separations decreases to the level of guessing (Nazir, 1992; Tripathy & Cavanagh, 2002), which is not observed in the case

of CI (e.g. Musilová et al., 2018; Simunovic & Calver, 2004; Wolford & Chambers, 1984). Moreover, the extent of peripheral CW is substantially larger than the extent of CI (Marten-Ellis & Bedell, in press; Song, Levi, & Pelli, 2014; and see comparisons of results of previous studies, e.g. Chung, Levi, & Legge, 2001; Musilová et al., 2018; Pelli, Palomares, & Majaj, 2004; Tripathy & Cavanagh, 2002). Peripheral CW and CI usually are explained on the basis of the substitution of flanker responses for the target or a pooling of the signals from the target and flankers (e.g. Dakin, Cass, Greenwood, & Bex, 2010; Ester, Zilber, & Serences, 2015; Freeman, Chakravarthi, & Pelli, 2012; Greenwood, Bex, & Dakin, 2009, 2010; Hanus & Vul, 2013). Moreover, CW is often considered as a more complex effect than CI, including other factors such as attention (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001; Strasburger, 2005) and, for stimuli presented at the fovea, inaccurate fixational eye movements (Bedell, Siderov, Formankiewicz, Waugh & Aydin, 2015; Flom, Weymouth & Kahneman, 1963; Stuart & Burian, 1962). Thus, peripheral CW seems dependent on multiple processes, some but not all of which may be similar to those that are responsible for CI.

It is possible that both CI and CW (in the fovea as well as peripherally) depend on more than one mechanism. Edge interactions are assumed to be relatively strong in the fovea and are considered as predominant in foveal CI. The additional contributions of response substitution and target-flanker pooling may account for possible differences between the results for CI and CW stimuli at the fovea. Response substitution and pooling are assumed to be much more powerful than edge interactions in the periphery, which would explain the greater magnitude and extent of peripheral CW than CI functions (which this study does not address).

The primary justification of this study was to compare foveal interaction for different CI and CW stimulus configurations, especially as evidence exists that CI and CW configurations produce dramatically different extents and magnitudes of interaction in the periphery. Varying the number and arrangement of flankers provides a simple method for varying the strength of the interactions (e.g., Bouma, 1970; Liu, 2001; Strasburger, Harvey, & Rentschler, 1991). If the mechanisms of foveal CW and CI are the same (and based mainly on center-surround receptive field antagonism, considered to be responsible for edge-to-edge interaction), the effects of the number and positions of letter and bar flankers should be similar. Otherwise, if one or more additional mechanisms contribute to foveal CW, then differences should exist for CW and CI stimulus configurations in both percent correct letter identification and in the

distribution of the observers' response errors. If the latter outcomes occur, then a secondary aim is to determine the extent to which the differences between foveal CW and CI can be attributed to response substitution and/or target-flanker pooling.

This study consists of two experiments. Experiment 1 focused on the dependence of CW and CI magnitude and extent on the target-to-flanker separation for different numbers of flankers. Experiment 2 focused on detailed examinations of the observers' responses, based on the analysis of confusion matrices. In addition, the influence of flanker complexity and similarity to the target letter on performance was studied for CW stimuli.

2. Methods

2.1 Observers

A total of 5 observers from two laboratories took part in this study. Two trained observers (PL and FP; 2 males, ages 23 and 37 years) participated in the experiment at Palacký University (PU) and 3 (HEB, NB and LM; 1 male and 2 females, ages 66, 64 and 33) at Anglia Ruskin University (ARU). Three of 5 observers were authors (FP, LM, HEB) and two were naïve. Observers were free from ophthalmic pathology or any systematic condition known to affect vision and had normal or corrected-to-normal vision. The study met the requirements of both of the institutional research ethics boards. The research at both universities was conducted in accordance with the tenets of the Declaration of Helsinki, and written informed consent was obtained from each observer before participating.

2.2 Stimuli

The stimuli were the same in both experiments. Black Sloan letters (C D H K N O R S V Z) were presented one at a time in random order on a white background, either in isolation or surrounded by 1, 2 or 4 high-contrast flankers under photopic conditions. Flankers were one of a selected set of Sloan letters (D, K, N, O) that differed from the central target (for CW), or one-stroke-width bars (for CI), presented at several separations measured from the innermost edge of the flanker to the outer edge of the central target (edge-to-edge) in accordance with several previous studies at the fovea (e.g., Bedell et al., 2013; Danilova & Bondarko, 2007; Flom, Weymouth, & Kahneman, 1963; Musilová et al., 2018; Siderov, Waugh, & Bedell, 2013). The limited number of

letter flankers was intended to facilitate a detailed analysis of the impact of each individual flanker. The set of flankers was selected to represent letters with high (N, D) and low (K, O) complexity (see Table 1, below), letters with side-symmetric edges (N), one-sided edges (D, K) and without straight edges (O), and letters with (K, N), and without sharp features (O), as well as a combination (D). The letter complexity was computed in accordance with Bernard & Chung (2011), as described in section 2.5, subsection *Effect of Flanker Complexity and Target-Flanker Similarity on CW*. For each presentation, the flanker letter was selected randomly from the set defined above. Single flankers were presented in the right, left, up or down position, 2 flankers were placed equally to the right and left (horizontally) or top and bottom (vertically) of the central target, and 4 flankers were equally spaced in all four directions. Examples of stimuli with different types, numbers and positions of flankers are presented in Fig. 1. Weber contrast of the stimuli was -92% at ARU and -97% at PU. The stimuli were generated using custom software developed by one of authors (FP) and displayed on a flat screen monitor. The LCD monitor at PU measured 22-in. diagonally, with 1680 x 1050 pixel resolution and a background luminance of 208 cd/m². A 13-in. monitor was used at ARU, with 1280 x 1024 pixel resolution and background luminance of 191 cd/m². The exposure duration of each stimulus was unlimited at both laboratories.

Fig. 1 about here

2.3 Procedure

Common procedure

In both experiments, testing was performed monocularly, with appropriate refractive correction, if needed. Stimuli were viewed foveally with the natural pupil. The observer identified each presented letter verbally and responses were entered by the operator using a PC keyboard into the experimental software, which stored the response together with information about the presented target and flanker. The viewing distance was 12 m at PU and 15 m at ARU; an optical quality mirror was used at both workplaces to achieve these distances. The size of the stimuli on the computer monitor was adjusted to achieve approximately 80% correct identification responses, when the letters were presented without flanking bars or letters.

The measurements obtained for each observer in both experiments were spread over several days, with breaks between the series of presentations each day

and when requested by the observer. Each series included 100 presentations with the same number, position, and type of flankers. Before the start of measurements, each observer was familiarized with the Sloan optotypes and the experimental procedure. Because the conditions were nearly identical at both workplaces, the data from both laboratories were processed together for each experiment.

Procedures for Experiment 1

All 5 observers participated in experiment 1. Across the 5 observers, the average letter size was 3.6 with a standard deviation 0.7 min arc. For each observer, percent correct letter identification was then determined in the absence of flankers and for 6 edge-to-edge target-flanker separations for all types, numbers and positions of flankers. Each condition included 100 stimuli presentations. The order of the different viewing conditions was pseudo-random. For each observer, edge-to-edge angular separations corresponded to 10, 20, 40, 60, 80 and 100% of the unflanked target letter size.

Procedures for Experiment 2

Four observers (FP, PL, NB and LM) took part in experiment 2. The average letter size was 3.8 with a standard deviation 0.6 min arc. We focused on two target-to-flanker edge-to-edge separations, 20% and 100% of letter size. The error rate for a separation of 20% separation was high enough to permit an analysis of miscalls, but remained significantly above guessing. A separation of 100% provided a condition, in which at least CI vanishes. For each type, number and arrangement of flankers we used the data from experiment 1 as well as the data from additional series of measurements to accumulate a total of either 1000 or 1100 presentations per observer. The exception was the one-bar-above condition at a separation of 100% letter size for observer NB, for which only 900 presentations were obtained because of a bookkeeping mistake. As in experiment 1, measurements were obtained as series of 100 presentations at both PU and ARU and the order of testing the different conditions was pseudo-random.

2.4 Data Analysis for Experiment 1

A three-factor repeated-measures ANOVA was performed on the results of the 5 observers to determine the main effects of separation, type of flankers (i.e., bars or

letters) and number of flankers and the interactions between these factors on percent correct letter identification. The factor “number of flankers” includes not only the number, but also position of flankers and therefore contains 7 categories (4 for one flanker, 2 for two flankers and 1 for four flankers). Departures from sphericity were insignificant (Mauchly sphericity test). Post hoc comparisons were realized using the Tukey honest significant difference (HSD) test. The significance level was set at 0.05. The analysis was performed using STATISTICA 13.0 (StatSoft, Tulsa, OK, USA).

To determine the magnitude and extent of CI and CW, we adopted the definition used previously by Musilová et al. (2018). For this purpose, the dependence of the value $p(s)$, percent correct letter identification, on the target-to-flanker separation, s , for each flanker type, number and position was fitted by a cumulative normal density curve with modified range in the form

$$p(s) = \gamma + (1 - \lambda - \gamma) \frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^s e^{-\frac{(t-s_0)^2}{2\sigma^2}} dt,$$

where e is the Euler's number ($e \approx 2.718$), s_0 and σ are the mean and standard error of the cumulative normal density function, and γ and $(1 - \lambda)$ are the lower and upper asymptotes of this function. The fitting of s_0 , σ , γ and λ (including estimation of their standard errors) was realised numerically using STATISTICA 13.0 (StatSoft, Tulsa, OK, USA). If γ was < 0.1 (i.e., the limit of guessing), it was fixed to 0.1. The magnitude M was defined as the difference between the upper asymptote and extrapolated percent correct value for the edge-to-edge separation $s = 0$, i.e., $(1 - \lambda) - p(0)$. The spatial extent of CW or CI was defined as the separation at which the percentage of correct responses decreases from the upper asymptote by M/e^3 (i.e., approximately by 5% of M). The standard errors (SE) of the estimated magnitudes and extents were numerically derived on the basis of common rule of propagation of uncertainties and the relevant 95% confidence intervals were computed as estimation $\pm 1.96SE$. Some previous studies (e.g., Tripathy & Cavanagh, 2002) defined the extent of CW as the separation at which the percentage of correct responses decreased from the upper asymptote by $1/e$ (approximately 37%) of the fitted curve's amplitude. This definition appears to underestimate the extent of CW and CI and can even be negative if the percentage of correct responses decreases very slowly. Our modified definition of extent precludes these problems.

2.5 Data Analysis for Experiment 2

We used a three-factor repeated-measures ANOVA to examine the influence of separation (100% and 20% of letter size), flanker type (bars and letters) and number of flankers (also including the flanker positions, as in experiment 1) as well as interaction effects on percent correct letter identification of the cumulative data of the 4 observers in experiment 2. All post hoc comparisons were realized using the Tukey HSD test with a significance level set at 0.05. The analysis was performed using STATISTICA 13.0 (StatSoft, Tulsa, OK, USA).

Confusion Matrices

Based on the data for the 20% target-to-flanker separation for the 4 subjects who took part in experiment 2, separate confusion matrices were constructed for each number and arrangement of flankers. Each confusion matrix was constructed by averaging the individual confusion matrices of the 4 observers and, therefore, was based on a total of at least 4,000 letter presentations. In each resulting confusion matrix, the rows specify the letter that was presented and the columns indicate the proportion of the aggregate responses corresponding to each of the 10 possible Sloan letters. Thus, the sum of the elements in each row equals 1. For CW, partial confusion matrices also were constructed separately for each of the 4 possible letter flankers (D, K, N, O).

Miscalls also occur when the target is presented without any flankers, based on simple letter confusions (SLCs), and can be represented by a SLC matrix. As very little or no CI or CW occur for an edge-to-edge target-to-flanker separation of 100% letter size (see the Results, below), all of the responses obtained using 100% target-to-flanker separations can be used to approximate the SLC matrix. Confusion matrices were constructed from each observer's CI and CW results for 100% target-to-flanker separation from all seven arrangements of flankers (i.e. 7 matrices per observer for CI as well as for CW) and the SLC matrix was approximated as the average. Therefore, the resulting SLC matrix was based on 56,200 letter presentations.

As the sum of row elements in each matrix is equal to 1, the element on the intersection of the row representing the target letter, T , and the column representing the response, R , also can be interpreted as an experimental probability P of response R for target T . The experimental probability of response R for the target T is denoted as $P_{CI}(T, R)$ when bar flankers are used (i.e. for CI) and $P_{CW}(T, R; F)$ for the letter

flanker, F (i.e., for CW with the flanker, F) or $P_{CW}(T, R)$ for data pooled across all letter flankers. The probability of response R for target T in the case of SLC is denoted as $P_{SLC}(T, R)$.

First, the confusion matrices for a separation equal to 20% of letter width were compared visually to study the relationship of CW and CI. Then, the Pearson's correlation coefficient r between the proportions of errors in the CI and CW matrices (with data pooled across all flankers and for each letter flanker separately), i.e., between $P_{CI}(T, R)$ and $P_{CW}(T, R; F)$ or $P_{CW}(T, R)$, where $T \neq R$, was computed for each number of flankers for an edge-to-edge target-to-flanker separation of 20% letter size. As we assume that CW includes edge-to-edge interaction represented by the CI matrix, a high correlation coefficient reflects a greater similarity between the relative error distributions in the CI and CW matrices and suggests that the mechanisms of both effects (i.e. CI and CW) are more similar than in the case of a low (or lower) correlation coefficient.

Effect of Flanker Complexity and Target-Flanker Similarity on CW

CW can also be influenced by the structure (represented, e.g., by complexity) and similarity of the target and flankers. Several related definitions of letter complexity appear in the literature (e.g., Bernard & Chung, 2011; Majaj, Pelli, Kurshan, & Palomares, 2002; Pelli, Burns, Farell, & Moore-Page 2006; Wang, He, & Legge, 2014; Zhang, Zhang, Xue, Liu, & Yu, 2009). We adopted the definition of complexity used by Bernard & Chung (2011), which is based on each letter's morphological skeleton. A morphological skeleton curve consists of the centres of all maximal circles inscribed within the object. We computed the complexity of each Sloan letter *relative to* the complexity of a bar flanker, i.e., as a ratio of the length of morphological skeleton of the letter to the length of morphological skeleton of a simple bar. For this purpose, each letter, as well as a bar, were inscribed separately within a square 200x200 pixel image and the skeleton was computed using the function "bwmorph" of the Image processing toolbox in MATLAB 6.5. The computed relative complexities of all Sloan letters are presented in Table 1.

Similarity S_{TF} between a target letter, T , and a letter flanker, F , was based on the SLC matrix (Freeman, Chakravarthi, & Pelli, 2012) and was defined as the decimal logarithm of the experimental probability (in %), that the isolated letter, T , would be misread as the letter, F , i.e., $S_{TF} = \log[100P_{SLC}(T, R)]$. The logarithm was used because

the $P_{SLC}(T, R)$ values were not distributed normally, but were skewed toward low values.

The possible effects of complexities C_F and C_T of flanker F and target T and target-flanker similarity S_{TF} on the change of percent correct response between the no-flanker condition (approximated by the diagonal elements $P_{SLC}(T, T)$ of the average SLC matrix) and the 20%-separation CW condition were evaluated using a multiple regression analysis in the form

$$P_{SLC}(T, T) - P_{CW,i}(T, T; F) = a \times C_F + b \times C_T + c \times S_{TF} + d.$$

The term $P_{CW,i}(T, T; F)$ denotes the percentage of correct responses for i -th observer and for target T when the letter flanker F is presented. The symbols a , b , c and d are regression coefficients. The goodness of fit of the whole model is represented by a coefficient of determination, r^2 . The individual data of the 4 observers from experiment 2 were pooled across all targets and flankers and used for this analysis. As CW for the one-flanker conditions was weak, only the 4- and 2-flanker conditions were analysed. The analysis was performed using STATISTICA 13.0 (StatSoft, Tulsa, OK, USA) with a significance level 0.05.

Table 1 about here

3. Results

3.1 Experiment 1

Fig. 2 presents the average values of percent correct letter identification averaged across all 5 subjects for all tested numbers and positions of flankers, plotted as a function of the edge-to-edge, target-to-flanker separation, expressed in terms of percent of letter width. Results in the case of letter flankers (i.e., CW) are in the top panel and for bar flankers (i.e., CI) are in the bottom panel. The individual data of each observer in the CW and CI conditions are provided as supplementary Figures, S1 and S2. The effects of CW and CI are shown by the reduction in percent correct letter identification with decreasing separation and are confirmed by a significant main effect of target-to-flanker separation ($F_{df=6, 24} = 61.639$, $p < 0.0001$).

Fig. 2 about here

Fig. 3 about here

The plots in both panels of Fig. 2 also show that increasing the number of flankers degrades target identification for both CI and CW stimuli, as indicated by a significant main effect of number of flankers ($F_{df=6, 24} = 22.675, p < 0.0001$). This effect is especially apparent for smaller target-to-flanker separations, as shown by a significant interaction between the number of flankers and separation ($F_{df=36, 144} = 12.033, p < 0.0001$), resulting from a systematic increase of the magnitude of CW and CI with increasing flanker number (see Fig. 3, top panel).

Although the main effect of flanker type was not significant ($F_{df=1, 4} = 5.155, p = 0.086$), significant interactions between flanker type and separation ($F_{df=6, 24} = 12.848, p < 0.0001$) and flanker type and number ($F_{df=6, 24} = 4.153, p = 0.0053$) show that letter flankers reduce the percentage of correct responses more than bar flankers, especially at small target-to-flanker separations and for a greater number of flankers. A significant difference exists between the results obtained with bar and letter flankers for stimuli with 4 flankers and with 2 top-bottom positioned flankers (post hoc Tukey HSD tests for flanker type x number-of-flankers interaction, $p = 0.00029$ and $p = 0.012$, respectively), but not for 2 right-left positioned flankers or any of the one-flanker conditions (post hoc Tukey HSD test, $p > 0.16$ for all comparisons).

The estimated magnitudes and extents, computed using the percent correct data averaged across all 5 subjects for different numbers and positions of flankers for CW and CI, are presented in Fig. 3 (magnitude in the top panel, extent in the bottom panel). In the case of CW, the magnitudes and extents were derived using data from all separations including the no-flanks condition. In the case of CI, the magnitudes and extents were derived using all separations including the no-flanks condition and also after excluding the data for 10% target-to-flanker separation, where a so-called upturn of the CI function may occur (see below). Respective 95% confidence intervals were derived except for some of the one-flanker CI conditions, for which the fitting algorithm returned degenerate (zero) *SEs* for some of the fitted parameters. The top panel of Fig. 3 indicates that the *magnitudes* of CI and CW are significantly different for the 4 flanker-condition and for both conditions with 2 flankers. The difference between the results obtained using bar and letter flankers appears to be connected with a reduction, or even a small upturn, of the slope of the percent correct performance function of CI at the smallest target-to-flanker separation (bottom panel of Fig. 2). No such effect is apparent for the same target-to-flanker separation when letter flankers are used (top panel of Fig. 2). Although a similar upturn occurs for the 2 flanking-bar condition, top

and bottom, but not for 2 flanking bars right and left, a significant difference of magnitude exists between CI and CW for both of the 2-bar flanking conditions (top panel of Fig. 3). Moreover, if the data representing the upturn are omitted, the mean estimates of CI magnitude are similar, suggesting that all observed differences between the magnitudes of CI and CW are not fully explained by an upturn of CI results.

The plots in Fig. 2 suggest that the *extent* of CW is larger than that of CI, especially for the 4-flanker condition. However, the plots in the bottom panel of Fig. 3 reveal no marked dependence of extent on the flanker type. For the 4-flanker condition, the difference in extent between CW and CI borders on significance.

3.2 Experiment 2

Experiment 1 revealed differences between CW and CI based on the arrangement and number of the flankers. The second experiment was performed to help explain the origin of these differences.

Repeated-measures ANOVA of percent correct letter identification for 100% and 20% target-to-flanker separations for the 4 subjects in experiment 2 yielded results similar to experiment 1. The results averaged across all 4 subjects for all tested numbers and positions of flankers are plotted for both edge-to-edge, target-to-flanker separations, expressed in terms of percent of letter width in supplementary Figure, S3. Plots for CW are in the top panel and for CI are in the bottom panel. The main effects of separation and flanker number were significant ($F_{df=1,3} = 56.523$, $p = 0.0049$; $F_{df=6,18} = 17.501$, $p < 0.0001$) as was their interaction ($F_{df=6,18} = 14.315$; $p < 0.0001$) and the interaction of type and number of flankers ($F_{df=6,318} = 3.832$; $p = 0.012$). The main effect of flanker type ($F_{df=1,3} = 0.013$, $p = 0.92$) was not significant. In contrast to experiment 1, the interaction of flanker type and separation also was insignificant ($F_{df=1,3} = 3.784$, $p = 0.15$) whereas the 3-way interaction of type, separation and number of flankers was significant ($F_{df=6,18} = 3.379$; $p = 0.021$). This interaction, together with supplementary Figure, S3, shows that CW is stronger than CI in the 4-flankers condition for a 20% target-to-flanker separation. The interaction is also supported by post hoc Tukey HSD tests, which show that letter flankers affect percent correct responses more than bar flankers only for 4 flankers at a separation of 20% (post hoc Tukey HSD test, $p = 0.0002$ for separation 20% and 4 flankers; $p > 0.11$ for other comparisons); in contrast, experiment 1 found differences also for 2 flankers located above and below the target. In comparisons of the data for 100% separation, the only

significant differences in percent correct were between 4 letter flankers and 2 right-left positioned letter flankers and between 4 letter flankers and 1 letter flanker positioned on the right and left ($p = 0.033$, $p = 0.040$ and $p = 0.023$, respectively). These results suggest that letter flankers have a slightly greater influence on performance than bar flankers for a 100% flanker-to-target separation; however, a direct post hoc comparison of CI and CW for 100% separation, pooled across all numbers and positions of flankers, did not achieve significance ($p > 0.088$).

The effects of CW for individual flanking letters are presented in Fig. 4 as a plot of percent correct identification vs. the flanker arrangement for 20% flanker-to-target separation. The biggest differences are between the flanker N and bar flankers in the 4-flanker condition, which suggests a substantial contribution of other effects to CW in addition to the putative edge-to-edge effect from CI. A marked difference also exists between 2 right-left positioned flankers N and O. To explore the data from experiment 2 in more detail, the observers' responses were examined using confusion matrices.

Fig. 4 about here

Confusion Matrices

Confusion matrices can help to identify specific differences between CI and CW responses and, thereby, potentially illuminate the mechanisms of origin of these effects. The confusion matrices for a flanker-to-target separation equal to 20% of letter size are shown for the CI and CW 4-flanker conditions in Fig. 5 together with an approximation of the SLC matrix. Fig. 6 presents separate confusion matrices for the 4-flanker CW conditions for the trials on which D, K, N and O was the flanking letter. The proportion of trials on which each letter was reported correctly lies on the main diagonal of each matrix. Values off the main diagonal represent the proportion of letter confusions per row (each corresponding to a different letter target), and are color coded from light blue to red to represent low vs. high proportions of letter confusions, respectively. The blank cells indicate combinations of presented letters and responses that did not occur.

Fig. 5 about here

Fig. 6 about here

Comparison of the matrices representing CI and CW for the 4-flanker condition (Fig. 5) shows that letters D, K and N were reported more frequently for CW compared to CI stimuli. The differences are evident especially if the CI matrix is compared with

matrices obtained for each individual flanking letter (Fig. 6) and probably represent response substitution errors. This effect is most marked for the flanker N, and less so for the flankers K and D. The smallest increase in response errors corresponding to the flanking letter, compared to the CI confusion matrix, occurs when the flanker is “O.” Inspection of Fig. 6 also indicates more miscalls of letters during CW that often are confused with the flanking letter (refer to the estimated SLC matrix, shown in Fig. 5). These miscalls can be explained by a combination of response substitution and SLC. For example, when the flanking letter during CW is N, there is an increase in miscalls, compared to the CI matrix, of “H” as well as “N”. The reduced number of substitution responses when the flanker is O may be attributable to the fact that O is the letter that is identified correctly least often (see the estimated SLC matrix in Fig. 5). On the other hand, there are other differences in the CW miscalls compared to CI, which cannot be explained readily by a combination of substitution and SLC, e.g., an increased number in miscalls of “D” (especially for target letter O) when the flanker is K. This result may be consistent with a target-flanker pooling effect, such that the vertical line in K is integrated with the target letter O to generate a composite percept similar to D. These errors also are apparent for both of the 2-flanker conditions; see supplementary Figures, S4 and S5. The round flanking letters, D and O, result in a big increase in responses of “V” for the target letter, Z. These miscalls are also apparent in the 4-flanker condition and when flankers are positioned at the top and bottom (although not when the two flankers are positioned right and left); see supplementary Figures, S4 and S5. These confusions are not readily attributed to either response substitution or target-flanker pooling. The strong additional effects (substitution, pooling and, potentially, others) suggest the reason that correct responses are lower for letters than for bars in the case of 4 flankers, as presented in Fig. 4. The lowest performance for flanker N (see Fig. 4) probably corresponds with the highest contribution of response substitution compared to other flankers. Next, the percent correct identification in CW is poor when the targets are N or O, see Fig. 5. This performance decrease is also apparent in the CI matrix and can be produced by high confusability of N with H and O with C and D; see the approximation of the SLC matrix in Fig. 5.

Confusion matrices for the CI and CW conditions with 2 flankers (supplementary Figures, S4 and S5) reveal differences between the right-left and top-bottom flanker positions. The distribution of miscalls generated when each of the individual flanking letters is positioned to the right and left (as well as when the miscalls for right-left

flankers are aggregated for all flanking letters) is similar to the right-left CI confusion matrix. On the other hand, CW confusion matrices when flanking letters K or N are in the top and bottom positions indicate biases consistent with response substitution errors. Responses consistent with substitution errors are less obvious when the top-bottom flanking letter is D and are essentially absent when the flanker is O. As both K and N contain vertically oriented contours on one or both sides, these flankers may produce stronger edge-to-edge interaction, and fewer response substitutions, when positioned to the left and right, compared to above and below the target letter. On the other hand, the part of the flanking letter O, which is closest to the target, is short and may have induced weaker edge-to-edge interaction compared to the bar flankers. Together with few or no substitution errors the weaker effects of the flanker O may explain the better performance compared to bar flankers and the marked difference between correct responses with N and O flankers, see Fig. 4. The same effects can also explain the better performance in the case of a single O flanker in both horizontal arrangements compared to a single bar in the same positions.

The 1-flanker confusion matrices (presented in supplementary Figures S6 – S9) show only low numbers of miscalls and do not indicate any big differences between flanker positions and types. The miscalls in the 1-flanker matrices seem not to be influenced by the identity of the flankers. However, the slight differences in observer's performance between bar and letter flankers D and K in the right and left position (see Fig. 4) can be explained by the asymmetric shape of these two letter flankers – if positioned on the right, the vertically oriented contours are closest to the target and would be expected to induce a stronger edge-to-edge interaction in comparison with a position of these flanking letters on the left.

The Pearson's correlation coefficient, r , between the proportion of errors in the confusion matrices representing CI and CW was computed for each arrangement of flankers for an edge-to-edge, target-to-flanker separation of 20% letter size and are presented in Table 2. All correlations were significant ($p < 0.0035$) except for the 4-flanker condition for flanking letter N ($r = 0.052$; $p = 0.64$). The lowest and second lowest correlations for flankers N and K correspond with stronger substitution effects for these flankers compared to the flankers D and O. As substitution effects are represented by markedly different error distributions than an edge-to-edge interaction, which is presumed to be mainly responsible for CI, the correlation between CI and CW matrices decreases with an increasing contribution of substitution errors. The overall

correlation is poorest for the 4-flanker condition and highest for 1-flanker condition, i.e., CW and CI miscalls are most similar when a single flanker is presented and become successively less so as the number of flankers increases. In the 2-flanker conditions, the correlation between CW and CI matrices is higher for flankers positioned to the right and left compared to above and below, consistent with observations made above in this section. As percent correct did not differ markedly between the right-left and top-down flanker positions, we interpret lower correlations in the up-down flanker condition to indicate that errors attributable to CI are reduced and replaced by miscalls resulting from effects such as response substitution and target-flanker pooling.

Table 2 about here

Effect of Complexity and Similarity of Target and Flankers on CW

The above analyses indicate that foveal CW consists of edge-to-edge interaction as well as substitution or pooling and other effects, in accordance with the arrangement of the flanker letters. It is known that peripheral CW, which also reflects mechanisms based on substitution and/or pooling, is influenced by the complexity and similarity of the target and flankers (e.g. Bernard & Chung, 2011; Chanceaux, Mathôt, & Grainger, 2014). Similarly, foveal CW could be at least partly affected by complexity and target-flanker similarity.

For the 4-flanker CW condition, neither the model as a whole (see Data Analysis for Experiment 2, above; $r^2 = 0.028$, $p = 0.26$) nor any of the individual model effects (target-flanker similarity, target or flanker complexity) were statistically significant ($p = 0.30$, $p = 0.097$ and $p = 0.94$). For pairs of flankers positioned to the right and left, multiple regression analysis shows significant effects of target-flanker similarity ($p = 0.0029$) and flanker complexity ($p = 0.0087$), both of which correlate positively with the increase in error rate compared to that estimated from SLCs. That is, an increase of either target-flanker similarity (determined from the estimated SLC confusion matrix) or flanker complexity was associated with a higher error rate than expected from simple letter confusions. The effect of *target* complexity was not significant ($p = 0.26$) and the coefficient of determination for the whole model was low, but statistically significant ($r^2 = 0.126$, $p = 0.003$) for the right-left positioned flankers. As the flanker N has the highest complexity and O the lowest, these regression results are consistent with a slightly greater magnitude of CW for flanker N compared to O in the right-left flanker arrangement (see Fig. 4). For flankers positioned above and below the target, only the

effect of target complexity was marginally significant ($p = 0.042$) and *negatively* correlated with an increase in error rate compared to that predicted by SLCs. However, for the condition with 2 flankers at the top and bottom, the coefficient of determination of the whole model did not achieve significance ($r^2 = 0.044$, $p = 0.094$).

4. Discussion

The main aim of this study was to compare foveal CW and CI for different numbers and positions of flankers to document differences in the manifestation and possible mechanisms of origin of these effects. In experiment 1, we found that increasing the number of flankers results in an increase in magnitude of both CI and CW. However, this effect was stronger for CW. Detailed analyses of observed miscalls in experiment 2 suggest that foveal CW includes edge-to-edge interactions, as in CI, with additional contributions from response substitution and target-flanker pooling. These additional contributions to CW, especially in the 4-flanker condition, can account for the stronger influence on performance of letter flankers compared to bars. Target and flanker complexity and target-flanker similarity appear to have relatively weak influences on foveal CW.

Effect of arrangement and type of flankers on magnitude and extent

Our results indicate that the degrading influence of both nearby bar and letter flankers on foveal letter identification increases with the number of flankers and results in increasing magnitudes of CI and CW (see Fig. 3). Previously, Liu (2001) reported that the magnitude of foveal CI is smaller when Landolt Cs are presented with 2 compared to 4 flanking bars. Our results indicate the effect of letter flankers is greater than bar flankers, especially for smaller target-to-flanker separations and as the number of flankers increases (see Fig. 3). Such differences were not reported in previous studies that compared CI and CW target configurations (Danilova & Bondarko, 2007; Norgett & Siderov, 2014). In particular, Norgett & Siderov (2014) observed that letter and bar flankers produce a similar deterioration of visual acuity in adult observers. However, in their study, CI and CW were compared for a target-to-flanker separation of 50% letter width. According to our results, the difference between the two types of flanker is noticeable only for separations smaller than 40% letter width, which would account for why it was not observed by Norgett & Siderov (2014). Danilova

& Bondarko (2007) measured foveal performance using Landolt rings as the target and either bars or Landolt rings as flankers. Their data indicate that performance improves for CI, but not for CW, at the smallest target-to-flanker separation they tested, which was less than 1 min arc. However, in contrast to our 4- and 2-flanker results, their results reveal little or no difference in the magnitude of foveal CI and CW (see Fig. 3 in the cited publication). Like the current study, Marten-Ellis & Bedell (in press) compared foveal CI and CW using Sloan letters surrounded by either 4 flanking bars or letters and reported an upturn in performance for CI, but not CW at the smallest target-to-flanker distance they tested. This upturn resulted in a smaller magnitude of foveal CI than CW. In the current study, a difference between CI and CW is apparent not only at the smallest, but also at the second smallest target-to-flanker separation tested, before an upturn of the CI function occurs. Further, the difference in performance between CI and CW for small target-to-flanker separations persists for the top-bottom flanker configuration, for which no upturn in the CI results is apparent (Fig. 2). These considerations indicate that the difference between CI and CW at small target-to-flanker separations can be explained by the upturn of the CI function only in part.

As mentioned in the Introduction, foveal CI is often explained on the basis of center-surround antagonism within neural receptive fields (e.g. Bedell et al., 2013; Danilova & Bondarko, 2007; Flom, Weymouth, & Kahneman, 1963; Musilová et al., 2018; Siderov, Waugh, & Bedell, 2013). This explanation is supported by the observation that the magnitude of foveal CI decreases at low luminance (Bedell et al., 2013; Marten-Ellis & Bedell, in press; Musilová et al., 2018), which is consistent with the diminution of the antagonistic receptive-field surround for low-luminance targets. A similar reduction in the magnitude of foveal CW was observed at low luminance (Marten-Ellis & Bedell, in press; Pluháček & Siderov, 2018), suggesting that foveal CW also could result from center-surround receptive field antagonism. However, if both foveal CI and CW result from the same receptive-field mechanism, it is unclear why CW should be influenced by the number of flankers differently than CI, or why the magnitude of CW at high luminance should be greater than that of CI, as was observed in our experiment 1. Siderov, Waugh, & Bedell (2014) showed that for flanker widths equal to or greater than 20% (or greater than 30%, see Bedell, Siderov, & Pluháček, 2019; Siderov, Pluháček, & Bedell, 2020) of the target letter width, flanker width does not influence CI significantly, except that an upturn at very small target-to-flanker

separations occurs only for narrow flanking bars. Although letter flankers are necessarily wider than (one stroke width) flanking bars, the results of Siderov et al. (2014) indicate that flanker width does not explain the lower percentage of correct responses observed for CW compared to CI. Thus, we hypothesize that the greater magnitude of and the stronger influence of number of flankers on foveal CW compared to foveal CI probably reflects the contributions of additional influences, such as response substitution and target-flanker integration, which become more apparent as the number of flankers is increased.

In contrast to magnitude, the extent (measured edge-to-edge) of foveal CW is, at most, only slightly greater than CI (see Fig. 3). The extents we observed for CW and CI in the 4-flanker condition correspond to most previously published data (e.g., Bedell et al., 2013; Danilova & Bondarko, 2007; Formankiewicz & Waugh, 2013; Lalor, Formankiewicz, & Waugh, 2016; Musilová et al., 2018; Pluháček & Siderov 2018; Siderov, Waugh, & Bedell, 2013; for an exception see Coates et al., 2018, who reported a much smaller extent of CW, possibly due to fixation-stability control).

Studies of peripheral CW (e.g., Bouma, 1970; Toet & Levi, 1992; Tripathy & Cavanagh, 2002) generally measure target-to-flanker separation and the extent of interaction from the center of the target to the center of the flanker (center-to-center). In contrast, both foveal CI and CW occur only within a similar angular edge-to-edge range of target-to-flanker separations, irrespective of the target size (e.g. Bedell et al., 2013; Musilová et al., 2018; Siderov, Waugh & Bedell, 2013 for CI; Danilova & Bondarko, 2007; Formankiewicz & Waugh, 2013; Pluháček & Siderov 2018 for CW; Marten-Ellis & Bedell, in press for CI and CW). This similarity would break down if foveal CI and CW results were plotted instead in terms of center-to-center spacing suggesting that, in the fovea, an edge-to-edge metric for CW is appropriate. Further, the very small difference in extent between foveal CW and CI suggests that the contributions of response substitution and target-flanker pooling, which act to increase the magnitude of foveal CW, must occur within approximately the same target-to-flanker separations as the edge-to-edge interaction that is presumed to be responsible for the bulk of CW and CI.

Contributions of contour interaction and additional effects to foveal crowding

In contrast with published models of peripheral CW (e.g., Ester, Zilber, & Serences, 2015; Freeman, Chakravarthi, & Pelli, 2012; Hanus & Vul, 2013), we

suppose that foveal CW includes the edge-to-edge interaction that apparently mediates CI. Our presumption that CI plays an important role in foveal CW is based on the similar characteristics of both of these effects, including their nearly identical extents and their analogous dependence on stimulus luminance (Bedell et al., 2013; Marten-Ellis & Bedell, in press; Musilová et al., 2018; Pluháček & Siderov, 2018). The conclusion that foveal CW, especially in the 4-flanker condition, results from CI along with additional effects that contribute also to CW in peripheral vision is supported by an inspection of our observers' confusion matrices and by the pattern of correlation coefficients between CW and CI error responses. As response substitutions and target-flanker pooling decrease percent correct responses compared to CI alone, these additional contributions satisfactorily explain the difference between CW and CI in 4-flanker condition in experiment 1.

For the 2-flanker conditions, response substitution contributes little, especially when flankers are in the top and bottom positions. According to the correlation results shown in Table 2, a pair of letter flankers on the right and left produces more CI than 2 letter flankers located above and below the target, which may be related to the shape of the flanking letters, as D, K and N each contain a bar on at least one side that would be expected to produce strong CI. Further, most of the target letters contain either the same number or fewer features at the top and bottom compared to the sides (the exceptions being Z and S) so, in most instances, features of the target are most proximal to flankers in the right-left positions. Because the overall percent correct, aggregated across the 4 different flanking letters, was not significantly different between the top-bottom and right-left flanker positions, we presume the reduced contribution of CI when flankers are above and below the target is compensated by an increase in substitution errors compared to the flankers in the right-left position.

When only a single letter flanker is present, CI accounts for most of the observers' errors. The differences in the contribution of CI for the 4 different flanker positions (see Table 2) seems to be closely connected with flanker shape. For example, a significant difference in the CI contribution between the conditions with a letter flanker on the right or left vs. top or bottom is most apparent in the results obtained with flankers N and K compared to more symmetrical flankers D and O.

As noted in section 3.1, above, we did not observe any significant difference in the overall percentage of correct response for vertically (top-bottom) and horizontally (right-left) located pairs of flankers in experiment 1, except between vertically and

horizontally positioned bars at the smallest target-to-flanker separation. This outcome agrees with the findings of Toet & Levi (1992), that the extent of the foveal crowding zone is approximately circular. On the other hand, Freeman (1980) observed that more response errors occur when observers read letter strings that are oriented vertically vs. horizontally. Freeman's observers read whole columns or rows of letters rather than a single target with either one or a pair of flanking targets as in both our study and the study by Toet & Levi (1992). As Freeman suggested, reading letters in rows vs. columns may be influenced by the extensive practice that most Western readers have with horizontally oriented reading material. In our experiment, with only one target and, at most two horizontal or vertical flankers, any practice effect should be minimized. We observed only differences in the distribution of miscalls with vertically vs. horizontally positioned letter flankers which, for the most part, can be explained by differences in edge-to-edge interaction according to the shape of the flankers or target letters, as discussed above.

Studies of peripheral CW found that more complex flankers more strongly impair visual performance than less complex flankers (Bernard & Chung, 2011; Chanceaux, Mathôt, & Grainger; 2014; but see Zhang et al., 2009, who reported stronger peripheral CW when the complexity of the flankers and target is similar). As letter flankers are more complex than bars (Table 2), this aspect of peripheral CW is consistent with our result that the magnitude of CW is greater than CI at the fovea. However, the effects of flanker and target complexity on foveal CW are not very clear. In experiment 2, we found a significant effect of flanker complexity and target-flanker similarity only for the condition of 2 flankers located to the right and left and a (weak) effect of target complexity only when 2 flankers are positioned above and below the target letter. Interestingly, in the 4-flanker condition, in which CW is strongest and includes the greatest contribution from response substitution, all complexity and similarity effects were insignificant. In the 2- and 4-flanker conditions of our experiments, all 4 flankers were the same, which could induce some grouping or pop-out effect that might reduce the influences of target-flanker similarity and flanker complexity. On the other hand, CW is strongest in the 4-flanker condition, with the largest contribution from response substitution, when the flanking letter is N, which is the most complex flanker. Thus, it seems that flanker complexity and target-flanker similarity may have affected foveal CW (with higher values of complexity inducing higher error rates, based on the results of our regression analysis), but these effects may have overlapped with those resulting

from other mechanisms. In general, the observed weak influences of target and flanker complexity and similarity may reflect that foveal CW depends more on the interaction of nearby edges, whereas peripheral CW does not.

Our study reveals differences between foveal CW and CI; in particular, that CW is a stronger phenomenon, especially for small target-to-flanker separations and for larger numbers of flankers. Detailed analysis of our observers' responses show that foveal CW reflects a mixture of CI and additional effects, such as response substitution and target-flanker pooling. The contributions of these different error components appear to vary according to the number and positions of the flankers; response substitution errors only contribute substantially in the 4-flanker condition and in the 2-flanker condition with flankers above and below the target. The additional effects of response substitution and target-flanker pooling can satisfactorily account for the differences between CI and CW and the observed dependence on flanker number.

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Fig. 1: Examples of a target (e.g., letter D) surrounded by different numbers and positions of flanking letters (e.g., K) for crowding (top) and by flanking bars for contour interaction (bottom).

Fig. 2: Percentage of correct responses for foveal crowding (top) and foveal contour interaction (bottom) averaged for all five observers and plotted as a function of the target-to-flanker, edge-to-edge separation in percent letter size; 100 percent letter size corresponds to an angular subtense of 3.6 min arc. The label, NF, on the x axis designates the no-flanker condition. Different symbols and lines represent different numbers and positions of flankers; see the key. The error bars represent standard errors across the 5 observers.

Fig. 3: Estimated magnitude (top) and extent (bottom) of CW and CI for four flankers (RLTB), two flankers right and left (RL) and top and bottom (TB), and one flanker right (R), left (L), top (T) and bottom (B). In the case of CW, the magnitudes and extents were derived using data from all separations including the no-flanks conditions. In the case of CI, the magnitudes and extents were derived using all separations including the no-flanks conditions and also when the data for the 10% target-to-flanker separation, where a so-called upturn may occur, were excluded (see the text for more details). The error bars represent the 95% confidence interval of the estimated values, when possible (see the text). Computed values are based on data averaged across 5 subjects.

Fig. 4: Percent correct letter identification averaged across 4 observers for each of the individual letter flankers used in this study in the case of four flankers (RLTB), two flankers right and left (RL) and top and bottom (TB), and one flanker right (R), left (L), top (T) and bottom (B). For comparison, data are shown also for each condition when bar flankers were used. The error bars represent standard errors of percent correct averaged across the 4 observers.

896

897 Fig. 5: Confusion matrices representing contour interaction (top left) and crowding (top

898 right) for the 4-flanker condition and a target-to-flanker separation equal to 20% of letter

899 width, and an approximation of the simple letter confusion (SLC) matrix (bottom left).

900 For details of how the matrices were constructed see the text. Blank cells indicate that

901 the specified letter-response combination did not occur. Color coding of the values in

902 the off-diagonal cells indicate relatively low (blue) to high (red) proportions of the

903 individual letter confusions.

904

905 Fig. 6: Separate confusion matrices for the 4-flanker crowding condition for trials when

906 D, K, N and O was the flanking letter (from top left to right bottom) at a target-to-flanker

907 separation equal to 20% of letter width. For details of how the matrices were

908 constructed see the text. Blank cells indicate that the specified letter-response

909 combination did not occur. Color coding of the values in the off-diagonal cells indicate

910 relatively low (blue) to high (red) proportions of the individual letter confusions.

911 Table 1: Relative complexity of each of the Sloan letters. Letters used as flankers are
 912 marked by asterisks.

Letter	C	D*	H	K*	N*	O*	R	S	V	Z
Relative complexity	2.12	2.47	2.58	2.29	2.65	2.00	2.96	2.85	1.92	2.61

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Table 2: Values of Pearson correlation coefficients between the proportions of errors in the contour interaction and crowding confusion matrices, for data pooled across all letter flankers and for each letter flanker separately, computed for each arrangement of flankers and an edge-to-edge target-to-flanker separation of 20% letter size.

	4 flankers	2 flankers right-left	2 flankers top-bottom	1 flanker right	1 flanker left	1 flanker top	1 flanker bottom
All flankers	0.415	0.769	0.484	0.889	0.828	0.709	0.740
Flanker D	0.625	0.890	0.534	0.859	0.833	0.871	0.855
Flanker K	0.321	0.668	0.512	0.945	0.845	0.678	0.733
Flanker N	0.052	0.672	0.325	0.867	0.784	0.586	0.580
Flanker O	0.727	0.854	0.571	0.889	0.899	0.735	0.782